female gland in the center of the mass. The prostate is oval, almost as long as wide, and granular. It connects with a long duct that narrows and expands again into the short ejaculatory portion of the deferent duct. The muscular ejaculatory portion opens into a common atrium with the vagina. The penis is unarmed. The vagina is very long and undulate. Near its proximal end it joins the elongate seminal receptacle, the uterine duct, and the rounded bursa copulatrix. The bursa copulatrix is stalked.

Remarks: Bergh (1877) first introduced the name *Spaherodoris papillata,* but without a description, and therefore it is a *nomen nudum* as of that paper. Later, Bergh (1878) described the species based on preserved specimens from the Philippines. Examination of the holotype revealed that the dorsum of this species is covered with numerous simple conical to rounded tubercles. The 48 mm-long specimen has 17 unipinnate branchial leaves. The features of this specimen fit with those of the specimen from Papua New Guinea here examined, and they are clearly conspecific.

Eliot (1904) described *Spaherodoris laevis* var. *variegata* based on a single specimen collected from Mnemba Island, Zanzibar, East Africa. The 31 mm-long animal was collected while laying a light violet-colored egg mass and had 14 branchial leaves. The color of the living animal was described as dark brown with greenish and sandy patches. The preserved specimen was mottled brown of darker and lighter shades and had bands formed of minute black spots, arranged in an irregular pattern, particularly near the branchial opening. Eliot (1904) described the dorsum of this species as having "irregular excrescences which resemble a marine growth." The radula had a formula 70 × 25.0.25. Eliot (1904) compared this animal to other specimens from Malaysia, "apparently referable to *S. laevis* [= *Actinocyclus verrucosus*]," which had the dorsum "quite smooth and of an almost uniform bluish-olive colour." In the same paper, he also mentioned another specimen collected from Mombasa, Kenya, which was different in color, but cannot be identified with certainty from the short description.

Eliot's (1904) description of *Spaherodoris laevis* var. *variegata* fits with the characteristics of the holotype of *Spaherodoris papillata* as well as with those of the specimen from Papua New Guinea. The brownish external color with irregular black lines, the number of branchial leaves, the abundance of large dorsal tubercles, and the radula formula are very similar.

Actinocyclus papillatus appears to be a different species from *A. verrucosus.* Externally, *A. papillatus* has more and larger tubercles than *A. verrucosus.* Also it has a number of ramified black lines on the dorsum that are absent in all specimens examined of *A. verrucosus.* Two specimens of *A. papillatus* (32 and 35 mm preserved length) have 14 branchial leaves, and one specimen 48 mm preserved length has 17 (Eliot, 1904; present paper), whereas smaller specimens of *A. verrucosus* (21 mm preserved length) have 16. A 38 mm-preserved-length specimen of *A. verrucosus* has 21 branchial leaves. Also, the gill of *A. papillatus* is pale brown or cream in color, whereas it is dark gray or black in *A. verrucosus.* In the reproductive system, the seminal receptacle of *A. papillatus* is more elongate than that of *A. verrucosus.* In addition, the ampulla and the prostate seem to be larger in *A. papillatus.* The radula of *A. papillatus* has more lateral teeth than that of *A. verrucosus,* for a specimen smaller in size. Eliot (1904) found a formula of 70 × 25.0.25 for a 31 mm-preserved-length specimen, the formula of the 35 mm-preserved-length specimen from Papua New Guinea is 69 × 29.0.29, whereas it is 65 × 15.0.15 in a 35 mm-preserved-length specimen of *A. verrucosus.* No variation has been found in the reproductive system of the three specimens of *A. verrucosus* examined.

Baba (1949) redescribed *A. laevis* var. *variegatus* from Japan and regarded it as different from *A. japonicus.* The external morphology of the single specimen was unknown. He found differences in the radular morphology and jaws. According to Baba, the inner radular teeth of *A. laevis* var. *variegatus* are longer and thinner than those of *A. japonicus.* Also, the jaw elements of *A. laevis* var. *variegatus* are simple, whereas those of *A. japonicus* may be simple or bifid. I have found a similar variation within a single specimen of *A. verrucosus.* The younger teeth normally look like those described by Baba (1949) for *A. laevis* var. *variegatus,* whereas the teeth from the middle of the radula are broader with longer denticles. However, the radular formula of Baba's specimen is 80 × 25–28.1.0.1.25–28 (for a 30 mm-preserved-length specimen), which is certainly very similar to formulae of our material of *A. papillatus.* It is very likely that his material actually belongs to *A. papillatus.* Baba (1949) also described several specimens of *A. japonicus,* which have a grayish brown dorsum, boldly variegated with black-brown, and all the dorsal tubercles tipped with black-brown. This description and the radular formula 120 × 30.1.0.1.30 fit with the characteristics of *A. papillatus,* and should probably be assigned to this species.

Hori & Fukuda (1996) described several specimens from Japan, under the name *A. japonicus,* that fit with the external morphology and anatomy of *A. papillatus.* The specimens have a pale background color with a number of dark, irregular, and ramified lines covering the entire dorsum, the gill is light brown or cream, and the radular formula is 80 × 22-30.0.22-30 for a 47 mm-preserved-length specimen.

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THE VELIGER

Owengriffithsius, a New Genus of Cyclophorid Land Snails Endemic to Northern Madagascar

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Abstract. *Owengriffithsius,* gen. nov. is diagnosed anatomically by its bursa copulatrix consisting of two adjacent ductless sacs; and by its bulbous-tipped penis in which the seminal tube is enclosed (no seminal groove), apically looped, and subapically opening, and which bears a thick, semicircular, flaplike gland. It is diagnosed conchologically by its concavely conic high spire with slightly mamillate apex; its V-channeled suture throughout ontogeny; its suturally notched double peristome; its relatively broad umbilicus (umbilical width/shell diameter 0.22–0.29 in known adults); its medium size (9.1–12.2 mm diameter in known adults); its periostracal hairs; its round and nearly planar outer peristome; and its horny, single-layered operculum. The genus contains six species and one subspecies, all of which are new and described herein. A dichotomous key is provided to their identification.

INTRODUCTION

This paper is one in a series reporting taxonomic results from the author's 1992–1996 survey and inventory of Madagascar's land mollusks (Emberton, 1998, 1999a, b, 2000, 2001, 2002, in press a, b, c, d; Emberton & Pearce, 1999a; 2000a, b, c).

METHODS AND MATERIALS

Materials were collected 1994–1996 using methods of Emberton et al. (1996). Identification and comparisons were made using Bequaert & Clench (1936), Wenz (1938–1944), Tielecke (1940), Morton (1952), Zilch (1959–1960), Solem (1959), Verdcourt (1963, 1964), Thompson (1969), Girardi (1978), Bruggen (1982, 1985, 1986, 1990), Fischer-Piette et al. (1993), and Emberton & Pearce (1999). Templeton's (1989) cohesion concept was applied in delimiting species. Geographically separated, morphologically discrete, extreme variants were deemed subspecies only if they seemed well isolated by discontinuous habitat.

Measurements were made using an ocular micrometer on a Wild M3C dissecting microscope. Dissections were on black wax under 70% ethanol, using procedures of Emberton & Pearce (1999: figures 32, 49, 50); anatomical descriptive terminology followed Girardi (1978). Photographs were taken at standard magnifications (×6.4, ×10, ×16, ×25, and ×40).

LOCALITIES

Of the 1126 stations collected throughout Madagascar in 1992–1996, only the following 17 stations—all northern—yielded ***Owengriffithsius,*** gen. nov.

74. Namoroka Reserve, 16°23′S, 45°20′E, 100 m, dry deciduous forest, 28 May 1995.

101, 102. Tsaratanana Reserve, 14°02′S, 48°47′E, rainforest. 101. 1100 m, 15 June 1995. 102. 1000 m, 16 June 1995.

206–213. Analamera Reserve, dry deciduous forest, 16 July 1995. 206, 208. 12°44′S, 49°30′E. 206. 195 m. 208. 100 m. 213. 12°44′S, 49°29′E, 30 m.

218. Montagne des Orchides, 12°23′S, 49°19′E, 385 m, dry deciduous forest, 20 July 1995.

405–407. Cap d'Ambre, Ambongoabo, 12°15′S, 49°15′E, 25 August 1995. 405, 406, baobab-deciduous forest. 405. 320 m. 406. 310 m. 407. 290 m, dry deciduous forest.

411. W of Sakaramy, S of Diego Suarez, 12°26′S, 49°12′E, 380 m, dry deciduous forest, 26 August 1995.

569–580, 803–807. Ankarana Reserve & vicinity, dry deciduous forest. 569. 12°56′S, 49°07′E, 130 m, 23 August 1995. 571. 12°57′S, 49°07′E, 85 m, dry deciduous forest, 24 August 1995. 577. 12°58′S, 49°06′E, 100 m, 25 August 1995. 580. 12°58′S, 49°05′E, 95 m, 26 August 1995. 803. 13°00′S, 49°01′E, 50 m, 8 October 1994. 807. 12°54′S, 49°06′E, 90 m, 10 October 1994.

SYSTEMATICS

Higher classification follows Ponder & Lindberg (1997; above superfamily) and Vaught (1989; superfamily and family). Latitudes and longitudes are given in degrees and minutes. To aid future workers, alcohol-preserved paratypes are listed separately, and species descriptions are ordered alphabetically. Types are placed in the Florida Museum of Natural History, University of Florida,

Gainesville (UF); the Australian Museum, Sydney (AMS); the Academy of Natural Sciences of Philadelphia (ANSP); and the Muséum National d'Histoire Naturelle, Paris (MNHN, which does not assign catalogue numbers to types).

Class GASTROPODA

Clade CAENOGASTROPODA

Clade ARCHITAENIOGLOSSA

Superfamily CYCLOPHOROIDEA

Family CYCLOPHORIDAE

Owengriffithsius Emberton, gen. nov.

(Figures 1–33)

Type species: ***Owengriffithsius capdaubrae***, sp. nov.

Other species and subspecies: ***O. capdaubrae aukaraaae***, subsp. nov., ***O. aualaaerae***, sp. nov., ***O. griffithsi***, sp. nov., ***O. naaorokae***, sp. nov., ***O. orchidae***, sp. nov., and ***O. tsaratanaae***, sp. nov.

Diagnosis: A cyclophorid genus unique anatomically in its combination of a bursa copulatrix consisting of two adjacent ductless sacs, and a greatly swollen seminal receptacle; and unique conchologically in its combination of a concavely conic high spire with slightly mamillate apex; a V-channeled suture throughout ontogeny; and, in adults, a suturally notched double peristome. Other diagnostic characters are its bulbous-tipped penis in which the seminal tube is enclosed (no seminal groove), apically looped, and subapically opening, and which bears a thick, semicircular, flaplike gland; and, conchologically, its relatively broad umbilicus (umbilical width/shell diameter 0.22–0.29 in known adults); medium size (known adults 9.1–12.2 mm diameter); periostracal hairs; evenly round, nearly planar, outer peristome; and horny single-layered operculum.

Spirostoma Heude, 1885, may possibly have a two-sacced bursa copulatrix (Tielecke's 1940: figure 11 is difficult to interpret), but has a much thinner seminal receptacle and an extremely different shell morphology.

Another undescribed genus from Madagascar (Emberton, unpublished) has a somewhat similar penial structure, but differs in its one-sacced bursa copulatrix and drastically different shell.

Conchologically, *Craspedotropis* Blanford, 1864, and *Japonia* (*Mylicotrochus*) P. & F. Sarasin, 1899, have concavely conic high spires, periostracal hairs, and broad umbilici, but lack both the sutural notch and the double peristome, and they have much more sharply angulate peripheries and peristomes.

Leptopoma Pfeiffer, 1847, is similar in shell size and shape, but has a much narrower umbilicus, only rarely has a double peristome, and lacks the deep sutural notch.

Laqocheilus Blanford, 1864, can look similar conchologically, but has much stronger spiral sculpture, a thicker peristome, and only a shallow sutural notch.

Cyclotus (*Millotorbis*) Fischer-Piette & Bedoucha, 1965, has a double peristome with sutural notch, a broad umbilicus, and periostracal hairs, but its spire is not concave, its outer peristome is non-circular and non-planar, and its shell size is minute (2.5–3.6 mm diameter).

Cyathopoma W. & H. Blanford, 1861, is likewise minute, lacks a sutural notch, and has a very different two-layered operculum.

Four species (***Owengriffithsius griffithsi***, sp. nov., ***O. naaorokae***, sp. nov., ***O. orchidae***, sp. nov., and ***O. tsaratanaae***, sp. nov.) are known only from dead-collected juveniles without opercula. Despite the absence of adult characters, they are clearly distinct, new species, and because they are so rare and unlikely to be collected as adults in the foreseeable future, they are described herein. Their placement in ***Owengriffithsius***, gen. nov. is based on the concavely conic high spire with slightly mamillate apex, the V-channeled suture throughout ontogeny, and the round aperture.

Among stylommatophorans (non-operculates), the valloniid (or vertiginid) *Pupisoma* Stoliczka, 1873, is somewhat similar to the latter four species in its aperture, sculpture, and roundish embryonic shell, but its umbilicus is minute, and its size is generally much smaller. If some past *Pupisoma* were to have continued growth with an increased whorl-expansion rate, however, it is conceivable that it evolved into one or more of the four species.

The enid orthurethran *Omphaloconus* (*Omphaloconus*) Westerlund, 1887, is similar in size and shape to ***Owengriffithsius griffithsi***, sp. nov., ***O. naaorokae***, sp. nov., ***O. orchidae***, ***sp. nov.***, and ***O. tsaratanaae***, sp. nov., but its aperture is much more elongate and its whorls concomitantly less rounded; its embryonic shell is asymmetrical and less mamillate; and its initial-post-embryonic sculpture seems to differ.

Description: Adult shell diameter 9.1–12.2 mm and probably down to about 6 mm, height/diameter of adults and juveniles 0.8–1.3, adult whorls 5.2–6.1, umbilicus/diameter 0.22–0.29 in known adults and down to 0.07 in juveniles. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery angulate, rounded, or bicarinate; suture deeply impressed, a V-shaped channel, beginning at shell's very apex. Aperture round, moderately capacious. Adult peristome double-lipped: inner lip unreflected; outer lip broadly and somewhat flatly reflected, but with a deep sutural notch, and narrow facing the umbilicus. Embryonic whorls 2.4–2.8; first 1.5 whorls 0.85–1.19 mm in diameter. Embryonic sculpture generally initially smooth, then with thin, dense axial riblets; rarely with axially oriented granulae instead. Body-whorl sculpture with axial, periostracal riblets or lamellae, the latter fringed densely with hairlike processes (usually worn off)

Figures 1–4. Dead-collected shells of ***Owengriffithsius capdambrae*** Emberton, gen. nov., sp. nov. Figure 1. Holotype in three views (UF 285461). Figures 2–4. Paratypes in one view: Figure 2, from type locality, Cap d'Ambre (UF 285460); Figures 3 & 4, from southwest of Diego Suarez (UF 285459, specimens #1 & #2 respectively). Scale bar 1 mm.

that are greatly elongate at the shell's—when present—peripheral angulation, carinae, and/or mid-basal spiral cord; or with minute, fairly evenly and densely spaced, somewhat wavy spiral cordlets.

Operculum fairly thin, horny, yellow with slight orangish tinge, circular, with parietal edge straight and rolled inward. Nucleus central. Opercular whorls gradually and evenly increasing, approximately equal in number to shell whorls. On both internal and external surfaces, whorls are rimmed with a thin low ridge. On external surface, about the third whorl and all subsequent whorls with extremely thin outer edges broadly overlapping subsequent whorls, producing a layered appearance. On internal surface, outermost whorl smooth and glossy, but all other surfaces somewhat rough and non-reflective.

Foot relatively short and broad, undivided. Snout (with

buccal mass unprotruded) short, divided centrally into two lobes. Protruded buccal mass (with mouth and radula showing) large, broad, rounded, un-notched, with no evident jaw, the two lobes of the snout appearing on the sides of its base like tiny lappets. Body gray, dorsal surfaces of the tentacles darker, snout lighter; mantle orangish cream with dark gray spattering. Testis large, nearly completely displacing apical digestive gland. Penis fairly long, thickly tubular, basally crooked, distally swollen and bulbous. Penial pore subapical, behind distal bulb, opening to side of penis. Ejaculatory duct coursing beneath surface of distal bulb and arcing backward before exiting at pore, and containing a long, muscular, terminal, invaginable, intromittant portion of penis. Within distal bulb of penis, on dorsal side, a white mass of glandular tissue is visible. Left side of penis bearing a smallish, thick, semi-circular, flaplike gland that rolls partially around penial shaft. Ovary lying along inside curve of apical digestive gland and consisting of tightly packed, bulbous acini. Oviduct (= "tube of FPSC" of Emberton & Pearce [1999]) with sharp, V-shaped bend before running alongside, then tapering into, seminal receptacle. Seminal receptacle (= "albumen gland" of Thompson [1969] = "glandular base of FPSC" of Emberton & Pearce [1999]) with slight-to-pronounced S-curve at its (proximal) junction with oviduct, thereafter C-shaped and greatly swollen, but tapering and straightening distally. Bursa copulatrix (= "seminal receptacle" of Thompson [1969] = "gland of FPSC" of Emberton & Pearce [1999]) consisting of two adjacent, ductless sacs, the upper (proximal) larger than the lower (distal).

Etymology: For Owen Griffiths of Mauritius, in recognition of his collection of, research on, and sponsoring of research on land snails, especially of Madagascar and the Mascarenes.

Gender: Masculine.

KEY TO SPECIES AND SUBSPECIES

1a. Initial whorl very small (diameter of first 1.5 whorls 0.85–0.87 mm); coiling very tight (whorls/ln diameter 3.52–4.56) 2
1b. Initial whorl larger (diameter of first 1.5 whorls 1.03–1.19 mm); coiling looser (whorls/ln diameter 2.49–3.47) 3
2a. Whorl periphery evenly rounded; umbilicus broader, 0.13–0.16 shell diameter .... ***O. griffithsi***
2b. Whorl periphery slightly angular; umbilicus narrower, 0.07–0.11 shell diameter ..... ***O. orchidae***
3a. Initial embryonic sutural channel granulate and with sutural radial marks; embryonic coiling tighter (diameter of first 1.5 whorls 1.03–1.04); general coiling also tighter (whorls/ln diameter 3.27–3.47) ..... ***O. namorokae***
3b. Initial embryonic sutural channel smooth and without sutural radial marks; embryonic coiling looser (diameter of first 1.5 whorls 1.10–1.19); general coiling also looser (whorls/ln diameter 2.49–2.83) 4
4a. Embryonic axial riblets dissected by dense, engraved spiral lines; body-whorl sculpture of minute, dense, parallel spiral cords; whorl periphery round, without angulation or carination ..... ***O. tsaratananae***
4b. Embryonic axial riblets simple, not crossed by spiral lines; body-whorl sculpture of one to three large spiral cords crossed by dense, hair-fringed riblets; whorl periphery angulate or bicarinate .. 5
5a. Embryonic whorls 2.6–2.8; tighter coiling (whorls/ln diameter 2.73 ..... ***O. analamerae***
5b. Embryonic whorls 2.4–2.5; looser coiling (whorls/ln diameter 2.49–2.65 6
6a. Whorl periphery with single angulation; four spiral color bands ..... ***O. capdambrae capdambrae***
6b. Whorl periphery bicarinate; no spiral color bands ..... ***O. capdambrae ankaranae***

DESCRIPTIONS OF SPECIES AND SUBSPECIES

Abbreviations: ad adult(s), frags fragments, juv juvenile(s).

Owengriffithsius analamerae Emberton, sp. nov.

(Figures 27–29)

Diagnosis: Most similar to ***O. capdambrae***, sp. nov., with which it shares (a) large initial whorl (diameter of first 1.5 whorls 1.10–1.19 mm); (b) loose coiling (whorls/ln diameter 2.49–2.83); (c) initial embryonic sutural channel smooth and without sutural radial marks; (d) embryonic axial riblets simple, not crossed by spiral lines; (e) body-whorl sculpture of one to three large spiral cords crossed by dense, hair-fringed riblets; and (f) whorl periphery angulate or bicarinate. ***O. analamerae***, sp. nov. differs from ***O. capdambrae***, sp. nov. in its greater embryonic whorl count (2.6–2.8 vs. 2.4–2.5) and in its tighter coiling (whorls/ln diameter 2.73 vs. 2.49–2.65).

Holotype: Station 213 (UF 285464, 1 ad).

Illustrated dry paratype: Station 206 (UF 285465, 1 ad, 1 juv).

Other dry paratypes: Stations 206 (UF 285470, 2 juv); 208 (AMS C.203499, 1 ad); 213 (UF 285471, 1 juv).

Type locality: Madagascar, Analamera Reserve, 12°44′S, 49°29′E, 30 m, dry deciduous floodplain forest, 16 July 1995.

Description of holotype shell (Figure 28; broken outer peristome): Male. Diameter 9.1 mm, height 8.0 mm, whorls 5.7, umbilicus 2.3 mm. Spire high, concave-conic, apex slightly mamillate. Body-whorl periphery angulate;

Table 1

Shell variation. Abbreviations: # specimen number, ColBnds color bands, D1.5W diameter of first 1.5 whorls, Diam shell diameter, EmW embryonic whorl count, fem female, Ht/D shell height divided by shell diameter, juv juvenile, med medium strength, Species/ss species or subspecies, Um/D umbilicus diameter divided by shell diameter, W/lnH shell whorl count divided by natural logarithm of shell height (= index of coiling tightness), Whls shell whorl count.

Species/ss	Catalog #	#	Sex	Diam	Ht/D	Whls	W/lnH	Um/D	D1.5W	EmW	ColBnds
analamerae	UF 285464	—	male	9.1	0.9	5.7	2.73	0.26	1.13	2.8	4 trace
	UF 285465	—	fem?	10.6	1.0	—	—	0.26	—	—	4 trace
	UF 285465	—	juv	—	—	5.2	—	—	1.13	2.6	4 trace
capdambrae	UF 285461	—	fem	12.2	0.8	6.1	2.65	0.29	1.13	2.5	4 faint
	UF 285460	—	male?	10.2	0.9	5.8	2.65	0.23	1.19	—	4 med
	UF 285423	1	fem	12.0	0.9	6.1	2.58	—	1.16	2.5	4 faint
	UF 285462	2	fem	11.7	0.8	6.0	2.62	0.25	1.15	2.5	4 med
	UF 285459	1	male?	10.9	0.9	6.0	2.60	0.22	1.18	—	4 trace
	UF 285459	2	fem	11.8	0.9	6.0	2.54	0.25	1.16	2.4	4 trace
	UF 285422	—	juv	—	—	4.8	—	—	1.15	2.5	4 med
ankaranae	UF 285463	—	fem	10.9	0.9	5.8	2.50	0.21	1.14	2.5	none
	MNHN	—	male	10.6	0.9	5.7	2.51	0.26	1.10	—	none
	AMS C.20350	0	fem?	11.0	0.9	5.9	2.58	0.24	1.10	2.5	none
	UF 285433	1	male	10.2	0.9	5.5	2.50	0.20	1.15	2.5	none
	UF 285434	2	fem	11.1	1.0	6.0	2.49	—	1.10	2.5	none
griffithsi	UF 285430	—	juv	3.2	1.3	5.0	3.52	0.16	0.86	2.5	none
	UF 285431	1	juv	2.4	1.2	4.5	4.29	0.13	0.85	2.5	none
	UF 285431	2	juv	1.9	1.2	3.6	4.56	0.14	0.87	2.5	none
namorokae	UF 285424	—	juv	3.8	1.1	5.0	3.47	0.08	1.03	2.5	none
	UF 285425	—	juv	3.7	1.2	4.9	3.27	0.11	1.04	2.5	none
orchidae	UF 285428	—	juv	2.8	1.2	4.6	3.87	0.07	0.85	2.5	none
	UF 285429	—	juv	2.3	1.1	4.0	4.35	0.11	0.85	—	none
tsaratananae	UF 285426	—	juv	5.4	1.1	4.9	2.77	0.11	1.13	2.5	none
	UF 285427	—	juv	4.8	1.2	4.9	2.83	0.19	1.13	2.5	none

suture deeply impressed, a V-shaped channel, beginning at shell's very apex; whorl shoulders flattish, gently rounded; earlier whorls with rounded shoulder. Aperture round, wide dorsal indentation; height 3.1 mm, width 3.4 mm; downward deflection moderate, 0.5 whorl. Peristome double-lipped: inner unreflected, outer broadly and somewhat flatly reflected, but with a deep sutural notch. Embryonic whorls 2.8; first 1.5 whorls 1.13 mm in diameter. Embryonic sculpture with first 1.2 whorls smooth, then thin, dense riblets. Body-whorl sculpture: faint, spiral, mid-basal cord; low, dense, fairly regularly spaced, axial riblets, with traces of fringing sharp hairs where uneroded, and traces of long broad hairs at peripheral angulation and in a baso-peripheral band. General color brown; white where periostracum eroded away; apex whitish, subsequent upper whorls dark purple-brown. Color bands four, trace, reddish brown: two above and two below peripheral angulation.

Shell variation: See Table 1 and Figures 27, 29.

Etymology: For Analamera Reserve.

Owengriffithsius capdambrae Emberton, sp. nov.

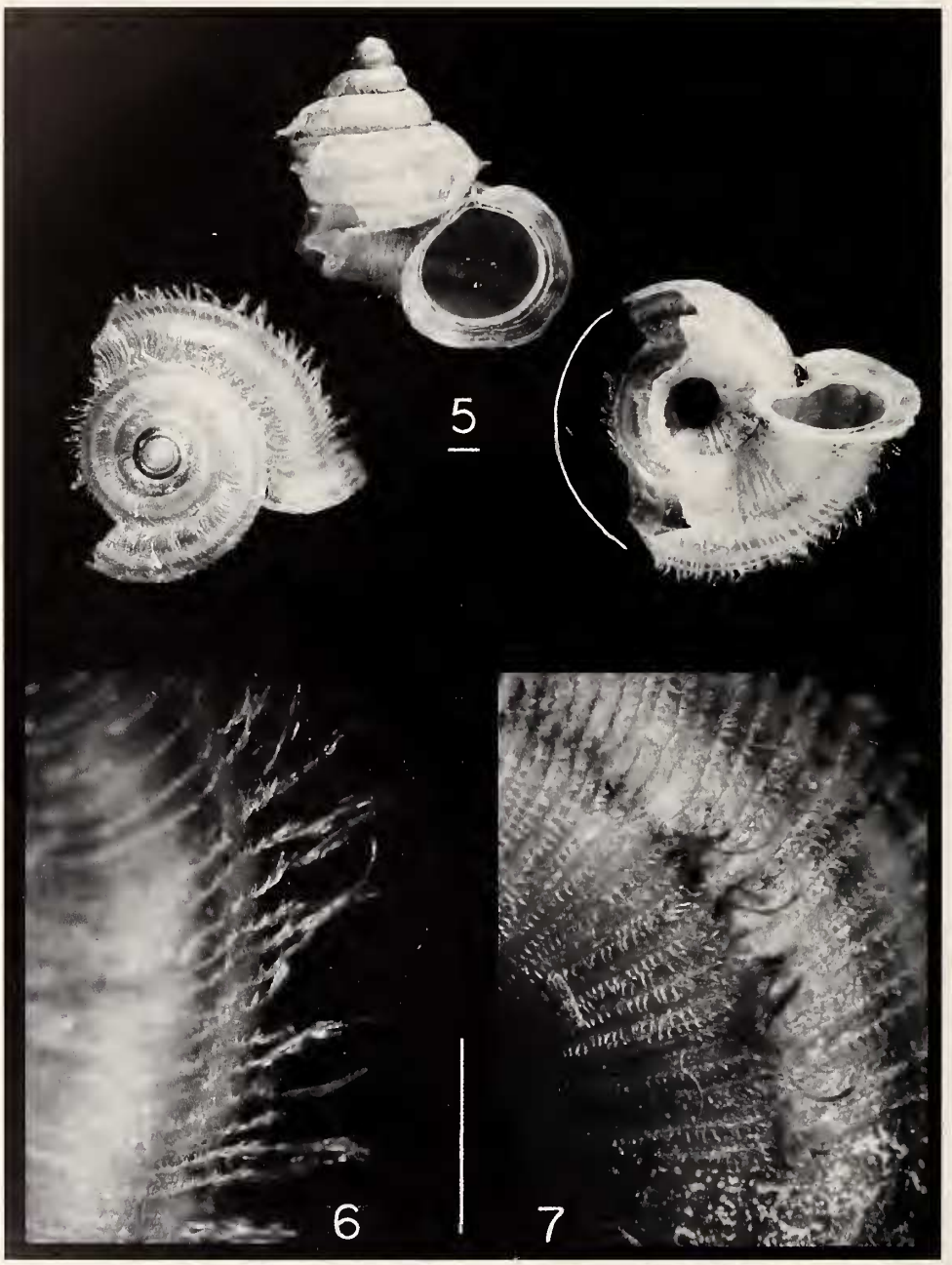
(Figures 1–14)

Diagnosis: Most similar to ***O. analamerae***, sp. nov., with which it shares (a) large initial whorl (diameter of first 1.5 whorls 1.10–1.19 mm); (b) loose coiling (whorls/ln diameter 2.49–2.83); (c) initial embryonic sutural channel smooth and without sutural radial marks; (d) embryonic axial riblets simple, not crossed by spiral lines; (e) body-whorl sculpture of one to three large spiral cords crossed by dense hair-fringed riblets; and (f) whorl periphery angulate or bicarinate. ***O. capdambrae***, sp. nov. differs from ***O. analamerae***, sp. nov. in its lesser embryonic whorl count (2.4–2.5 vs. 2.6–2.8) and its looser coiling (whorls/ln diameter 2.49–2.65 vs. 2.73).

Holotype: Station 407 (UF 285461, 1 ad).

Illustrated dry paratypes: Stations 407 (UF 285462, 1 ad [shell frag and operc from UF 285586]); 411 (UF 285459, 2 ad); 569 (UF 285422, 1 juv).

Illustrated alcohol paratypes: Station 407 (UF 285586, 2 ad [dissected]).

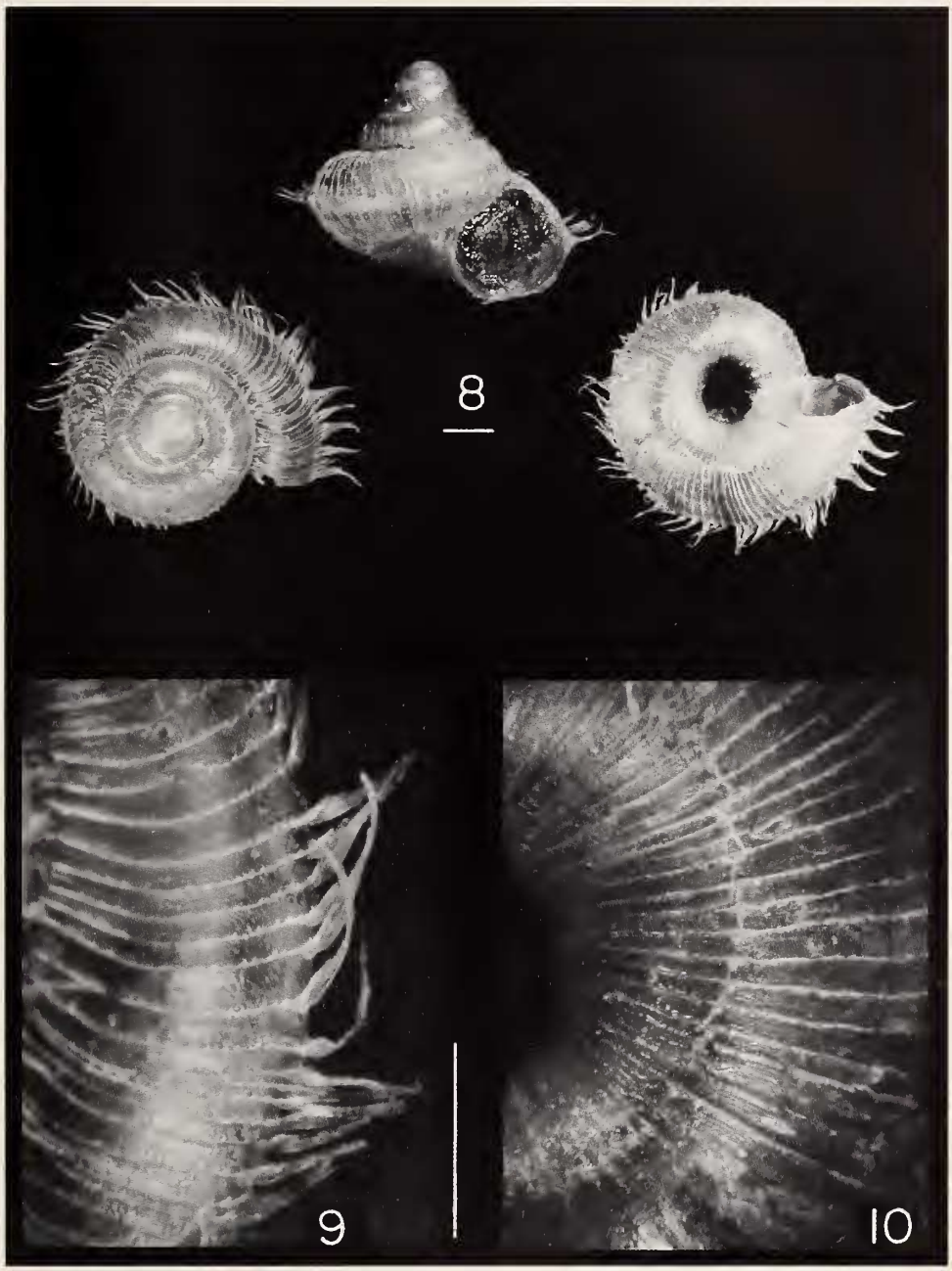


Figures 5–7. Live-collected shell of ***Owengriffithsius capdambrae*** Emberton, gen. nov., sp. nov., paratype from type locality, Cap d'Ambre (UF 285462). Figure 5. Whole shell (broken) in three views. Figures 6, 7. Magnifications of body whorl from dorsal and ventral aspects, respectively. Scale bars 1 mm.

Other dry paratypes: Stations 405 (UF 285584, 3 ad, 3 juv); 406 (UF 285583, 1 ad); 407 (AMS C.203501, 1 ad; ANSP 407928, 1 ad; MNHN, 1 ad; UF 285423, 1 ad [shell frags from UF 285586]; UF 285460, 1 ad [shell frags from UF 285586]; UF 285585, 7 ad, 5 juv); 411 (UF 285582, 2 ad, 3 juv); 571 (UF 285581, 1 juv).

Type locality: Madagascar, Cap d'Ambre, Ambongoabo, 12°15′S, 49°15′E, 290 m, dry deciduous forest, 26 August 1995.

Description of holotype shell (Figure 1): Female. Diameter 12.2 mm, height 10.0 mm, whorls 6.1, umbilicus 3.5 mm. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery angulate; suture deeply impressed, a V-shaped channel, beginning at shell's very



Figures 8–10. Fresh-dead-collected juvenile shell of ***Owengriffithsius capdambrae*** Emberton, gen. nov., sp. nov., paratype from type locality, Ankarana Reserve (UF 285422). Figure 8. Whole shell in three views. Figures 9, 10. Magnifications of body whorl from dorsal and ventral aspects, respectively. Scale bars 1 mm.

apex; whorl shoulders flattish, gently rounded; earlier whorls with rounded shoulder. Aperture round, wide dorsal indentation; height 3.8 mm, width 4.1 mm; downward deflection moderate, 0.3 whorl. Aperture double lipped: inner unreflected, outer broadly and somewhat flatly reflected, but with a deep sutural notch, and narrow facing the umbilicus. Embryonic whorls 2.5; first 1.5 whorls 1.13 mm in diameter. Embryonic sculpture: first 1.4 whorls smooth, then thin, dense riblets. Body-whorl sculpture: faint, spiral, mid-basal cord; low, dense, fairly rergularly spaced, axial riblets. with traces of fringing sharp hairs where uneroded behind apertural lip. General color brown; white where periostracum eroded away; apex whitish, subsequent upper whorls dark purple-

Figures 11–14. Opercula and anatomy of ***Oweugriffithsius capdambrae*** Emberton, gen. nov., sp. nov. type-locality females. Figure 11. Operculum of specimen #2 (UF 285462, ex UF 285586) in exterior, interior, and side views (left to right, respectively). Figure 12. Operculum of specimen #1 (UF 285423, ex UF 285586) in exterior view. Figures 13, 14. Body and oviduct-plus-seminal receptacle-plus-bursa copulatrix (removed from the uterus) of specimen #1 (UF 285586). Scale bars 1 mm.

brown. Color bands four, faint, reddish brown: two between suture and peripheral band of hairs, two between peripheral and baso-peripheral bands of hairs.

Shell variation: See Table 1 and Figures 2–10. As seen in very fresh shells (Figures 5–10), throughout ontogeny each axial lamella fringed with minute, evenly and densely spaced, sharp-pointed hairs that are uniform in size except over shell's peripheral angulation and mid-basal spiral cord, where hairs are extremely large and long, forming conspicuous fringing bands around shell. Hairs are readily lost, however, from older weathered shells, and even from shells that are relatively fresh (Figures 1–4).

Operculum (Figures 11, 12): Fairly thin, horny, yellow

with slight orangish tinge, circular, with parietal edge straight and rolled inward. Nucleus central. Whorls gradually and evenly increasing, approximately equal in number to the shell whorls. On both the internal and external surfaces, the whorls are rimmed with a thin low ridge. On external surface, about the third whorl and each subsequent whorl with extremely thin outer edge broadly overlapping next whorl, producing layered appearance. On internal surface, outermost whorl smooth and glossy, but all other surfaces somewhat rough and non-reflective.

Anatomy (Figures 13, 14, ethanol-fixed and -preserved): Foot relatively short and broad, undivided. Protruded buccal mass (mouth and radula showing) large, broad, rounded, un-notched, with no evident jaw, and with two lobes of snout appearing on sides of its base like tiny lappets. Body gray, dorsal surfaces of tentacles darker, snout lighter; mantle orangish cream with dark gray spattering. Ovary lying along inside curve of apical digestive gland and consisting of tightly packed bulbous acini. Oviduct with a sharp V-shaped bend before running alongside, then tapering into, seminal receptacle. Seminal receptacle with a pronounced S-curve at its (proximal) junction with the oviduct, thereafter C-shaped and greatly swollen, but tapering and straightening distally. Bursa copulatrix consisting of two adjacent, ductless sacs, the upper (proximal) slightly larger than the lower (distal).

Etymology: For Cap d'Ambre (Tanjona Bobaomby).

Owengriffithsius capdambrae ankaranae Emberton, subsp. nov.

(Figures 15–26)

Diagnosis: Differs from parent species in its bicarinate (vs. single-angulate) whorl periphery and its lack of spiral color bands (vs. four spiral color bands). Known only from Ankarana Reserve, where it is isolated from parent species by uninhabitable savannah.

Holotype: Station 577 (UF 285463, 1 ad).

Illustrated dry paratypes: Stations 577 (AMS C.203500, 1 ad; MNHN, 1 ad); 580 (UF 285433, 1 ad, 1 operc [shell frags from UF 285594]; UF 285435, 1 juv).

Illustrated alcohol paratype: Station 580 (UF 285594, 2 ad [dissected]).

Other dry paratypes: Stations 577 (UF 285592, 1 ad, 7 juv); 580 (AMS C.203502, 1 juv; UF 285434, 1 ad [shell frags from UF 285594]; UF 285593, 14 juv); 803 (ANSP 407929, 1 juv; UF 285591, 17 juv); 807 (MNHN, 1 juv; UF 285590, 15 juv).

Type locality: Madagascar, Ankarana Reserve, 12°58′S, 49°06′E, 100 m, dry deciduous forest, 25 August 1995.

Description of holotype shell (Figure 15; outer peristome broken along columellar edge): Female. Diameter 10.9 mm, height 10.2 mm, whorls 5.8, umbilicus 2.3 mm. Spire concave-conic, apex slightly mamillate. Body-whorl periphery roundish, bluntly bicarinate; suture deeply impressed, a V-shaped channel, beginning at shell's very apex, filled in part by carinal sculpture; whorl shoulders gently rounded. Aperture round, wide dorsal indentation; height 3.8 mm, width 3.9 mm; downward deflection great, 0.4 whorl. Peristome double lipped: inner unreflected, outer broadly and somewhat flatly reflected, but with a deep, narrow, sutural notch, and narrow facing the umbilicus. Embryonic whorls 2.5; first 1.5 whorls 1.14 mm in diameter. Embryonic sculpture: first 1.2 whorls smooth, then thin riblets. Body-whorl sculpture with three spiral cords, or carina: two peripheral and one mid-basal; crossed by fairly regularly spaced, moderately dense, axial, periostracal lamellae; lamellae are low, erect, with serrated edges, becoming clusters of tall, back-curved spikelets where they cross the spiral cords (Figures 18, 19). General color yellowish light brown; apex light reddish brown.

Shell variation: See Table 1 and Figures 16, 17. A fresh juvenile shell (Figures 20, 21) shows sculpture similar to adult holotype, but with carinal hairs much longer.

Operculum (Figure 22): As in parent species.

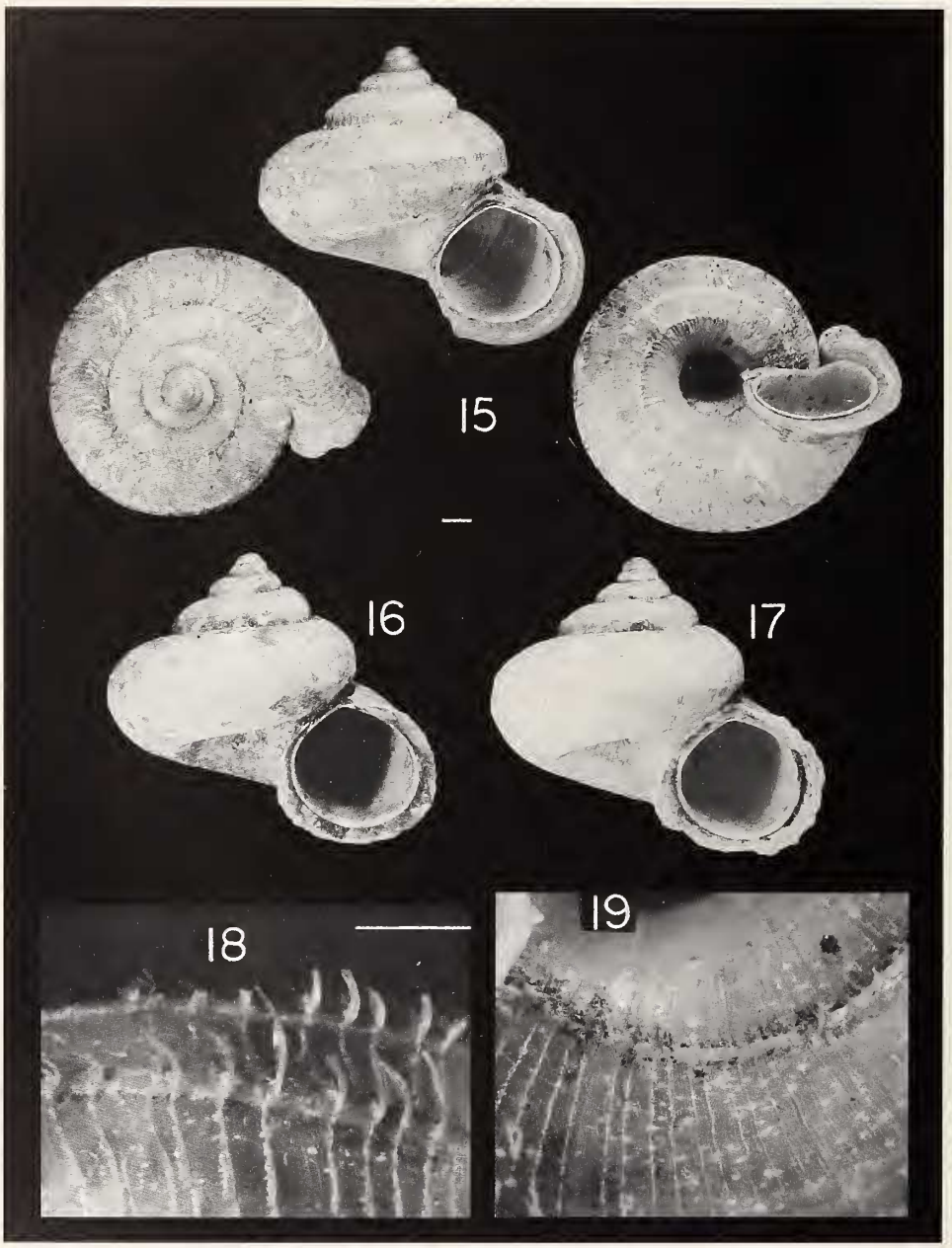
Anatomy (Figures 23–26, ethanol-fixed and -preserved): Foot and body as in parent species, but mantle virtually without darker spattering. Snout (with buccal mass unprotruded) short, divided centrally into two lobes. Testis large, nearly completely displacing apical digestive gland. Penis about 4.5 mm, thickly tubular, basally crooked, distally swollen and bulbous. Penial pore subapical, behind distal bulb, opening to side of penis. A longitudinal cross-section of the penis (not illustrated) indicates that ejaculatory duct courses beneath surface of distal bulb, arcs backward before exiting at pore, and contains a long, muscular, terminal, invaginable, intromittant portion of penis. Within distal bulb of penis, on dorsal side, a white mass of glandular tissue visible. Left side of penis bearing a smallish, thick, semicircular, flaplike gland that rolls partially around penial shaft. Female reproductive system as in parent species, except that oviduct and seminal receptacle are less tightly convoluted, and upper (proximal) of bursa-copulatrix sacs much larger than lower (distal).

Etymology: For Ankarana Reserve.

Owengriffithsius griffithsi Emberton, sp. nov.

(Figure 31)

Diagnosis: Most similar to ***O. orchidae***, sp. nov., with which it shares a very small initial whorl (diameter of first 1.5 whorls 0.85–0.87 mm) and very tight coiling (whorls/ln diameter 3.52–4.56). ***O. griffithsi***, sp. nov. differs from ***O. orchidae***, sp. nov. in its evenly rounded (vs.



Figures 15–19. Shells of ***Owengriffithsius capdambrae ankaranae*** Emberton, gen. nov., sp. nov., subsp. nov. Figure 15. Holotype (dead-collected) in three views (UF 285463). Figures 16, 17. Paratypes (dead collected) from type locality (AMS C.203500 and MNHN respectively). Figures 18, 19. Magnifications of body whorl from dorsal and ventral aspects, respectively, of live-collected paratype (UF 285433). Scale bars 1 mm.

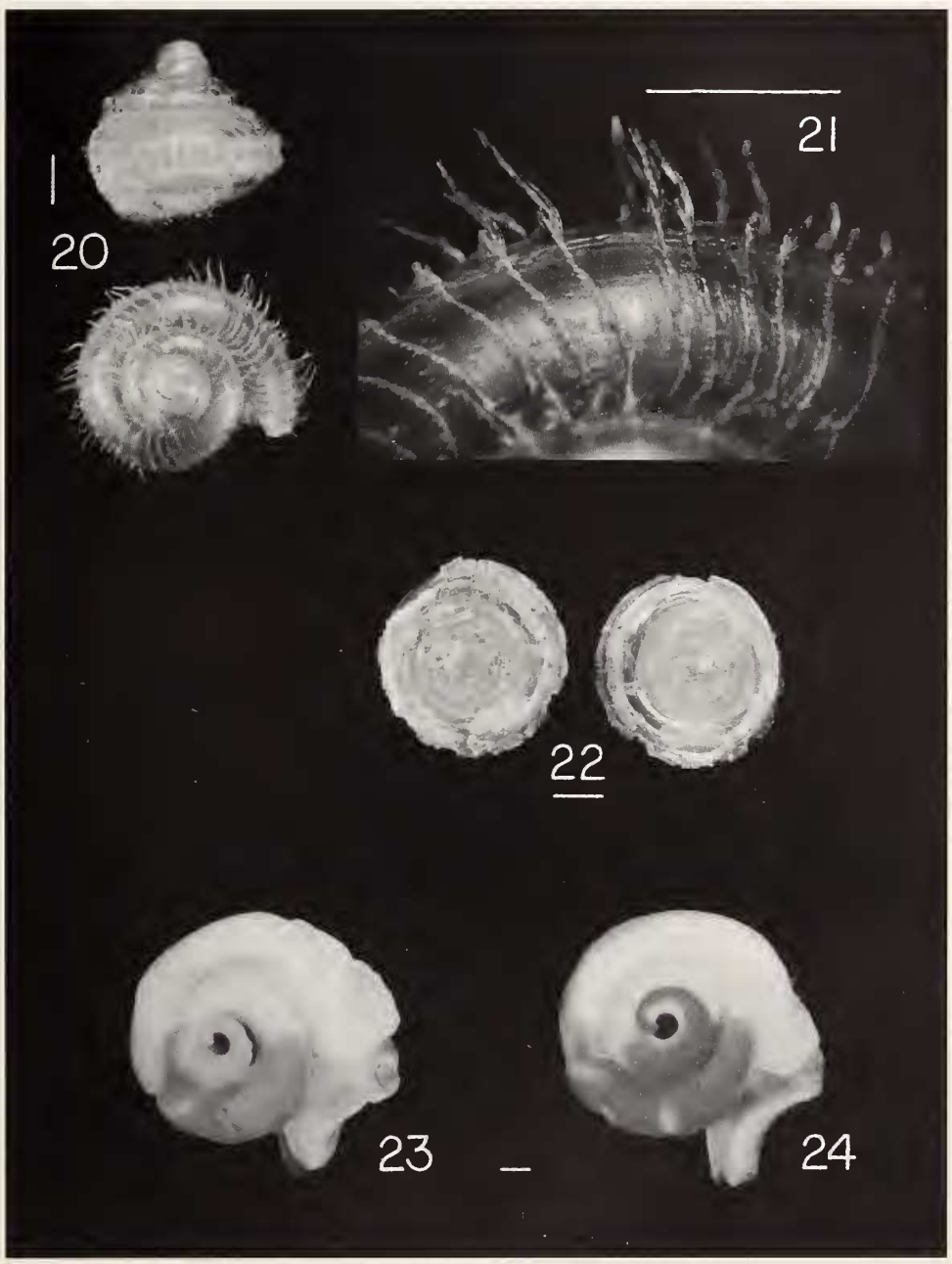
slightly angular) whorl periphery and in its broader umbilicus (0.13–0.16 shell diameter vs. 0.07–0.11 shell diameter).

Holotype: Station 803 (UF 285430, 1 juv).

Dry paratypes: Stations 803 (AMS C.203503, 2 juv; ANSP 407930, 1 juv; UF 285431, 4 juv); 807 (UF 285432, 1 juv).

Type locality: Madagascar, Ankarana Reserve, 13°00′S, 49°01′E, 50 m, 8 October 1994.

Description of holotype shell (Figure 31; weathered, broken; measurements taken at latest complete aperture): Juvenile. Diameter 3.2 mm, height 4.1 mm, whorls 5.0, umbilicus 0.5 mm. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery round; suture

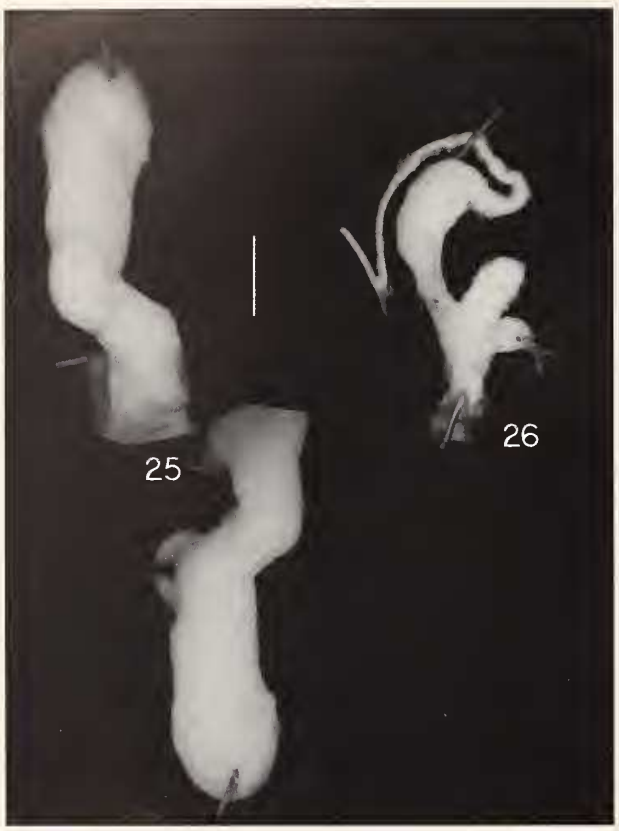


Figures 20–24. ***Owengriffithsius capdambrae ankaranae*** Emberton, gen. nov., sp. nov., subsp. nov. paratypes. Figures 20, 21. Fresh-dead-collected juvenile shell in two views and magnification of dorsal body whorl (UF 285435). Figure 22. Adult operculum in external and internal views (left and right, respectively; UF 285433, ex UF 285594 specimen #2). Figures 23, 24. Adult bodies (UF 285594): Figure 23, male (specimen #1); Figure 24, female (specimen #2). Scale bars 1 mm.

deeply impressed, a V-shaped channel, beginning at shell's very apex; whorl shoulders rounded. Aperture apparently round; height 1.8 mm, width 1.6 mm. Apertural lip unreflected, except slightly at columella. Embryonic whorls 2.5; first 1.5 whorls 0.86 mm in diameter. Embryonic sculpture: initial 1.7 whorls smooth, then densely and regularly spaced, thin-edged low riblets. Body-whorl sculpture smoothish, with transverse growth striae, uneven in spacing and in strength, but thin-edged and somewhat riblet like. Color uniform grayish white.

Shell variation: See Table 1.

Etymology: For Owen Griffiths, collector of this species.



Figures 25, 26. Reproductive organs of ***Owengriffithsius capdambrae ankaranae*** Emberton, gen. nov., sp. nov., subsp. nov. paratypes (UF 285594). Figure 25. Penis in dorsal and ventral views (upper and lower, respectively; specimen #1). Figure 26. Oviduct-plus-seminal receptacle-plus-bursa copulatrix (removed from the uterus; specimen #2). Scale bar 1 mm.

Owengriffithsius namorokae Emberton, sp. nov.

(Figure 32)

Diagnosis: Among the species of ***Owengriffithsius***, gen. nov. having a relatively large initial whorl (diameter of first 1.5 whorls 1.03–1.19 mm), ***O. namorokae***, sp. nov. is unique both in its tight coiling (whorls/ln diameter 3.27–3.47 vs. 2.49–2.83) and in having its initial embryonic sutural channel granulate and with sutural radial marks (vs. smooth and without sutural radial marks).

Holotype: Station 74 (UF 285424, 1 juv).

Dry paratype: Station 74 (UF 285425, 1 juv).

Type locality: Madagascar, Namoroka Reserve, 16°23′S, 45°20′E, 100 m, dry deciduous forest, 28 May 1995.

Description of holotype shell (Figure 32; aperture broken; measurements taken at latest complete aperture): Juvenile. Diameter 3.8 mm, height 4.2 mm, whorls 5.0, umbilicus 0.3 mm. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery slightly angular; suture deeply impressed, a V-shaped channel, beginning at shell's very apex; whorl shoulders rounded. Aperture apparently round; height 2.0 mm, width 1.9 mm; no downward deflection. Apertural lip unreflected, except slightly at columella. Embryonic whorls 2.5; first 1.5 whorls 1.03 mm in diameter. Embryonic sculpture: initial 1.2 whorls smooth except for sutural channel, which appears granular, thereafter completely granular with traces of axial orientation; initial whorl also with sutural radial marks. Body-whorl sculpture smoothish, with faint, parallel, fairly evenly and densely spaced, somewhat wavy spiral cordlets, and with faint, irregular axial growth striae; cordlets absent on base. Color uniform grayish white.

Shell variation: See Table 1.

Etymology: For Namoroka Reserve.

Owengriffithsius orchidae Emberton sp. nov.

(Figure 33)

Diagnosis: Most similar to ***O. griffithsi***, sp. nov., with which it shares a very small initial whorl (diameter of first 1.5 whorls 0.85–0.87 mm) and very tight coiling (whorls/ln diameter 3.52–4.56). ***O. orchidae***, sp. nov. differs from ***O. griffithsi***, sp. nov. in its slightly angular (vs. evenly rounded) whorl periphery and its narrower umbilicus (0.07–0.11 shell diameter vs. 0.13–0.16 shell diameter).

Holotype: Station 218 (UF 285428, 1 juv).

Dry paratypes: Station 218 (AMS C.204775, 1 juv; ANSP 407931, 1 juv; MNHN, 1 juv; UF 285429, 2 juv).

Type locality: Madagascar, Montagne des Orchides, 12°23′S, 49°19′E, 385 m, dry deciduous forest, 20 July 1995.

Description of holotype shell (Figure 33; aperture broken; measurements taken at latest complete aperture): Juvenile. Diameter 2.8 mm, height 3.3 mm, whorls 4.6, umbilicus 0.2 mm. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery slightly angular; suture deeply impressed, a V-shaped channel, beginning at shell's very apex; whorl shoulders rounded. Aperture apparently round; height 1.5 mm, width 1.5 mm; no downward deflection. Apertural lip unreflected, except slightly at columella. Embryonic whorls 2.5; first 1.5 whorls 0.85 mm in diameter. Embryonic sculpture: initial 1.8 whorls smooth, then strong, dense, regularly spaced, sharp-edged riblets. Body-whorl sculpture consisting of low, sharp axial riblets, sparsely and unevenly spaced, uneven in strength. General color light brown, apex whitish.

Shell variation: See Table 1.

Etymology: For Montagne des Orchides.

Figures 27–29. Shells of ***Owengriffithsius analamerae*** Emberton, gen. nov., sp. nov. Figure 27. Paratype in three views (UF 285465, specimen #1). Figure 28. Holotype in three views (UF 285464). Figure 29. Magnification of juvenile paratype (UF 285465, specimen #2). Scale bars 1 mm.

Owengriffithsius tsaratananae Emberton, sp. nov.

(Figure 30)

Diagnosis: Among the species of ***Owengriffithsius*** gen. nov. having (a) large initial whorl (diameter of first 1.5 whorls 1.10–1.19 mm), (b) loose coiling (whorls/ln diameter 2.49–2.83), and (c) initial embryonic sutural channel smooth and without sutural radial marks, ***O. tsaratananae***, sp. nov. is unique for its (a) embryonic axial riblets dissected by dense, engraved spiral lines; (b) body-whorl sculpture of minute, dense, parallel spiral cords; and (c) whorl periphery round, without angulation or carination.

Holotype: Station 101 (UF 285426, 1 juv).

Dry paratypes: Station 102 (AMS C.204504, 1 juv; ANSP 407932, 1 juv; MNHN, 1 juv; UF 285427, 5 juv).